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Source: Wildlife Biology, 2020(2)

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/wlb.00594

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Wildlife Biology 2020: wlb.00594
doi: 10.2981/wlb.00594

Subject Editor: Bogdan Cristescu. Editor-in-Chief: Ilse Storch. Accepted 30 January 2020

Pack size in humanized landscapes: the Iberian wolf population

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Group living is an important behavioral feature in some species of mammals, although somewhat uncommon in the Order Carnivora. Wolves *Canis lupus* are highly social and cooperative carnivores that live in family groups, i.e. packs. The number of wolves in a pack affects social, reproductive and predatory behavior, thus conditioning population dynamics. Despite its relevance to management decisions, pack size has not been thoroughly studied in populations inhabiting human dominated landscapes such as the Iberian Peninsula. We estimated variation of wolf pack size from 1990 to 2018 in northern Spain, both in winter and summer. Winter data corresponded to direct observations and snow tracking at 42 localities (n = 253 data, 160 pack-years), whereas summer data corresponded to observations at rendezvous sites at 22 localities (n = 237 data, 43 pack-years). We estimated average pack size from the largest number of wolves recorded at each locality and year. Winter pack size averaged 4.2 ± 1.7 (mean ± SD) individuals. At summer rendezvous sites adult/subadult wolves (older than one year) averaged 3.1 ± 1.3 individuals, whereas pups averaged 4.0 ± 1.9. Generalized linear mixed models (GLMM) showed that pack size declined through the winter from 4.9 (4.2–5.6, 95% CI) wolves in November to 3.8 (2.9–4.9, 95% CI) wolves in April. We found no trend in pack size, neither in winter nor in summer. We discuss our results compared with other studies and populations worldwide, and its usefulness to comprehend the dynamics of this vulnerable population.

Keywords: *Canis lupus*, grey wolf, pack size, rendezvous sites, winter

Group living is a behavioral characteristic in some mammalian species, but in the Order Carnivora only 10–15% species live in groups, a strategy that entails specific selective pressures (Creel and Macdonald 1995). In social and cooperative species of carnivores, most individuals live in social units (i.e. groups, packs, clans, prides) with complex dynamics that affect parameters such as litter size, pup and adult survival, dispersal and, ultimately, population dynamics; group size can also influence prey choice, kill rates and interactions among conspecifics and with other species. In addition, reproductive output can be determined by group living through reproductive suppression of subordinate individuals (Macdonald and Kays 2005).

Wolf populations are organized in cooperative social units named packs (Mech and Boitani 2003). Packs of wolves are highly territorial and maintain exclusive areas by means of visual, olfactory and acoustic communication. Their basic composition is a breeding pair, the dominant male and female that usually monopolize reproduction, plus their offspring and other adults or sub-adult wolves (Mech 1999). Wolf pack size ranges from two to more than twelve individuals, and varies seasonally from lower in late winter to higher in summer after parturitions (Mech and Boitani 2003). It may also vary widely among populations (Fuller et al. 2003), and variation in pack size is one of the determinants of wolf population size (Hayes and Harestad 2000, Fuller et al. 2003, Apollonio et al. 2004), together with prey biomass and territory density (Kittle et al 2015, Mech and Barber-Meyer 2015). Pack size variation and composition affects pup survival and reproductive success (Harrington et al. 1983, Peterson et al. 1984), as well as kill rates, food intake, predation rates and interactions with neighboring groups (Vucetich et al. 2002, Metz et al. 2011).

The cohesiveness of individuals within a pack has been related to the capability of killing large prey, and the outcome of competition with scavengers (Schmidt and Mech

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1997, Vucetich et al. 2004). Cohesion among wolves in a pack is affected by the number of individuals, the composition of the group (i.e. age and sex of the members), the season, and also by abiotic factors like snow depth (Fuller 1991, Mech and Boitani 2003). Pack cohesion can influence the estimates of pack size, and thus ultimately of population size (Chapron et al. 2016). Estimates of pack size have been commonly derived from direct observations, or counting the track-sets of packs in snow (e.g. compilation by Fuller et al. 2003), and more recently from non-invasive genetic sampling at rendezvous sites and along tracks (Stenglein et al. 2011, Liberg et al. 2012). Nevertheless, potential factors affecting the counts of individuals in packs as well as variation and uncertainty have not often been described in detail (Fuller et al. 2003, Barber-Meyer and Mech 2015).

A currently isolated wolf population inhabits humanized landscapes of the Iberian Peninsula, in Spain and Portugal (Chapron et al. 2014). The population, which includes about 350 wolf packs (MAGRAMA 2016, Torres and Fonseca 2016), is strictly protected in Portugal (listed as Endangered, Cabral et al. 2005), and is under culling and hunting management in most of its Spanish range (Quevedo et al. 2019). Several authors have discussed pack size in this population (Barrientos 2000, Llaneza et al. 2009, Fernández-Gil et al. 2010, Blanco and Cortés 2012, Fernández-Gil 2013) but evaluation of determinants and variability of pack size are generally lacking. Our goals were estimating average pack size and evaluating its seasonal and long-term variation by using direct observations and track sets, while exploring factors that could affect those estimates.

Material and methods

Study areas

We collected data at 42 and 22 localities in the winter and summer areas, respectively. Winter data were gathered in the Cantabrian Mountains and nearby highlands, while summer data were collected in the Duero Plateau and Montes de León mountain range near the border with Portugal (Fig. 1). Several summer localities were less than 50 km away from winter locations, while western and easternmost winter localities were more than 200 km apart (Fig. 1).

The Cantabrian Range and Montes de León hold seminatural areas of deciduous forests interspersed with shrublands up to the subalpine level (1800 m a.s.l.), and pastures where extensive livestock grazing is an important activity. The Duero Plateau is an agricultural steppe averaging 800 m a.s.l. with remnants of sub-Mediterranean forests of oak and pine. It harbors extensively managed sheep flocks, and livestock farms. In the Cantabrian Range and Montes de León wolves feed upon wild (red and roe deer, wild boar, chamois, ibex) and, to a lesser extent, domestic ungulates, whereas in the

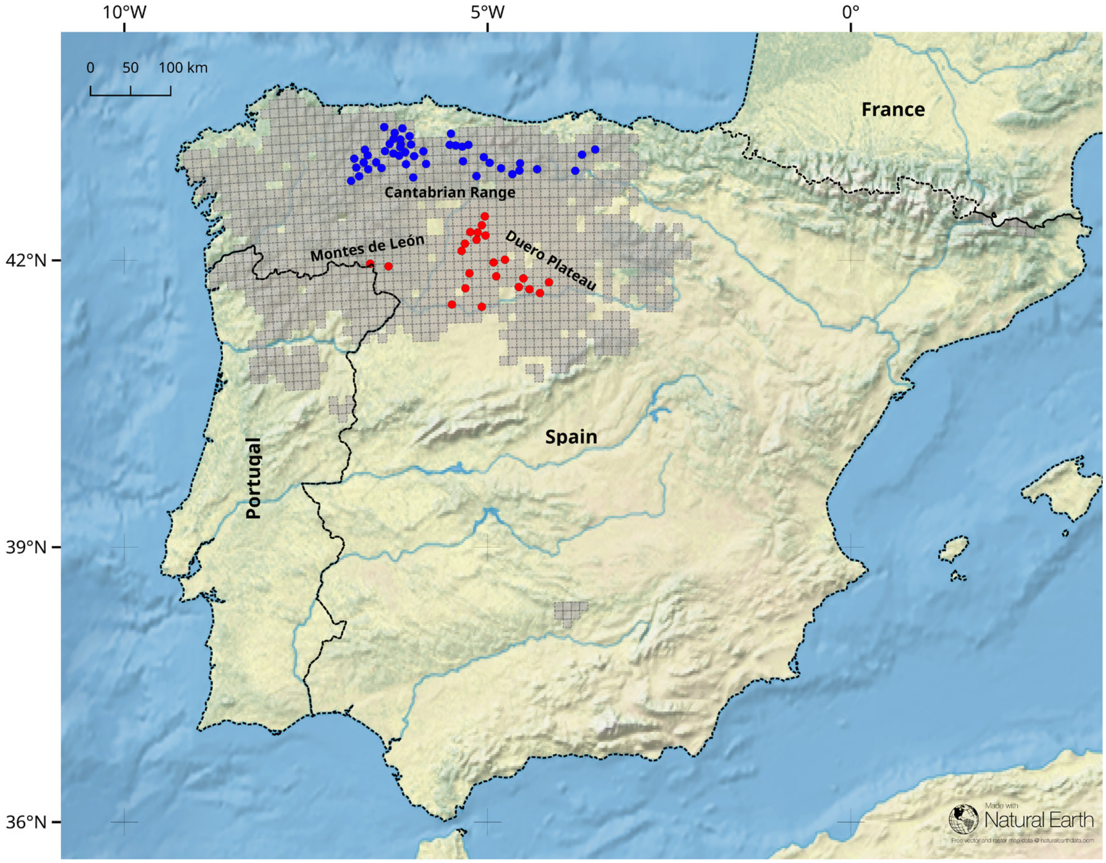

Figure 1. Localities included in the study. Winter data (blue dots) were collected in the Cantabrian Range (n = 42 localities), while summer data (red dots) were collected in the Duero Plateau and Montes de León mountain range (n = 22 localities). Grey shading shows a 10 × 10 km grid covering the approximate distribution of the Iberian wolf population in Spain and Portugal (sensu Chapron et al. 2014).

Duero Plateau carrion farm offal is an important diet source alongside ungulates (roe deer, wild boar) and Lagomorpha (Cuesta et al 1991).

Winter data

We collected wolf observations from 2000 to 2018 in winter, between November and April, i.e. between the abandonment of rendezvous-sites (the places where pups are fed until they can travel with the rest of the pack) and the births of the following breeding season.

We collected data on winter travelling packs (sensu Messier 1985, Ballard et al. 1995), i.e. the number of wolves travelling together (Schmidt et al. 2008), a metric commonly used in demographic studies of wolves (Fuller et al. 2003). We searched for track sets in the snow and used spotting scopes at dawn to look for wolves from vantage points. We focused on areas regularly used by wolves, mostly ridges, mountain passes and unpaved roads. We retained for analyses observations that met the following criteria: 1) direct observation of two or more travelling wolves lasting at least 10 min; 2) track sets on snow of at least 1 km including at least two wolves (i.e. the minimum number of wolves in a pack; Fuller et al. 2003, Ausband et al. 2014). Criteria to determine the number of individuals through direct observations and snow tracks were thus roughly equivalent in terms of traveled distances (Frame et al. 2004). We discarded for example observations of lone wolves, unclear or short track sets or observations of resting packs. All winter data were collected by either one of two observers: any locality could be searched by any of both, but at different dates. Each record included the number of individuals, location, date, observer and method (direct observation versus snow tracking). We used vantage points consistently and searched for snow track sets at specific locations; thus for a given combination of pack and year we assumed that data obtained at a specific location and year belonged to the same pack.

Data on snow cover were gathered from the NASA National Snow and Ice Data Center (Hall and Riggs 2016a, b). Snow cover was measured at each pack location and closest available date (i.e. maximum of eight days of difference) as the proportion of terrain covered by snow in 500 m cells and, when data was missing at that resolution, in 0.05° cells (about 4.3 × 5.5 km). Data on snow depth was not available.

Summer data

We collected direct observations at rendezvous sites between 1990 and 2002, from July to October. In the Iberian Peninsula, pups are usually born in late May, and remain at the den for up to five weeks (Vilá et al. 1995, Packard 2003); hence, pups are hardly seen before July. They can travel with the adults about mid-October, then abandoning rendezvous sites or using them solely as daily resting spots. We watched for wolves in areas where signs of intense use had been detected (e.g. heavily used trails with tracks and scats). Observations were conducted by a unique observer from vantage points at dawn or dusk, using spotting scopes, usually from 2 km or more to avoid disturbances. We considered two age classes because of their different behavior, attendance of rendezvous sites, and summer movement patterns (Packard 2003): pups (up to five months old), and adults/sub-adults (older than one year) can be easily differentiated by size overall aspect.

Variables and data analyses

We hypothesized that some methodological factors can affect the counts of individuals in a pack, e.g. counting method (two classes in winter) and observer; estimates can also be affected by abiotic factors (snow) that influence cohesion among individuals in a pack. We looked for long term trends by using year as a continuous variable along the studied periods in summer and winter. We also expected that the number of wolves in a group would decrease along both seasons because of mortality and dispersion, so we considered the month in which data were gathered as predictor, either as continuous (linear effects) or as a categorical (non-linear effects) variable (Table 1). We fitted generalized linear mixed models (GLMM; Poisson error distribution, log link function) to the number of wolves (n wolves) as response variable in winter, and observer, method, month, year and snow cover as predictors. We excluded from analysis those records lacking reliable data on snow cover. In summer, we fitted separate models to the number of adults and sub-adults, and pups (n ads and n pups, respectively), using month and year as predictors. We entered locality as random factor in all GLMMs. We used Akaike information criteria (AIC) and AIC weight (AICw) for model selection (Burnham and Anderson 2004, Burnham et al. 2011). Models were fitted using R package lme4 (Bates et al. 2015, <www.r-project.org>). We computed an autocorrelation function 'acf' in R

Table 1. Description of variables considered in generalized linear mixed models (GLMMs).

	Description	Season
Variables		
n wolves	No. of wolves per pack in each observation	winter
n ads	No. of adult wolves (>1 year) seen in each observation at a rendezvous site	summer
n pups	No. of pups seen in each observation at a rendezvous site	summer
Predictors		
month (cont.)	Continuous; November to April in winter (n = 6), July to October in summer (n = 4)	summer and winter
month (factor)	Categorical; three classes of two months each in winter; two classes in summer (two months each)	summer and winter
year	Continuous; n = 19 (winter), n = 13 (summer)	summer and winter
method	Categorical; two levels: direct observation versus snowtracking	winter
observer	Categorical; two levels (observers)	winter
snow.cover	Continuous; % snow cover at the date and locality of each observation	winter
locality (random factor)	Specific locality, i.e. territory, of each observation	summer and winter

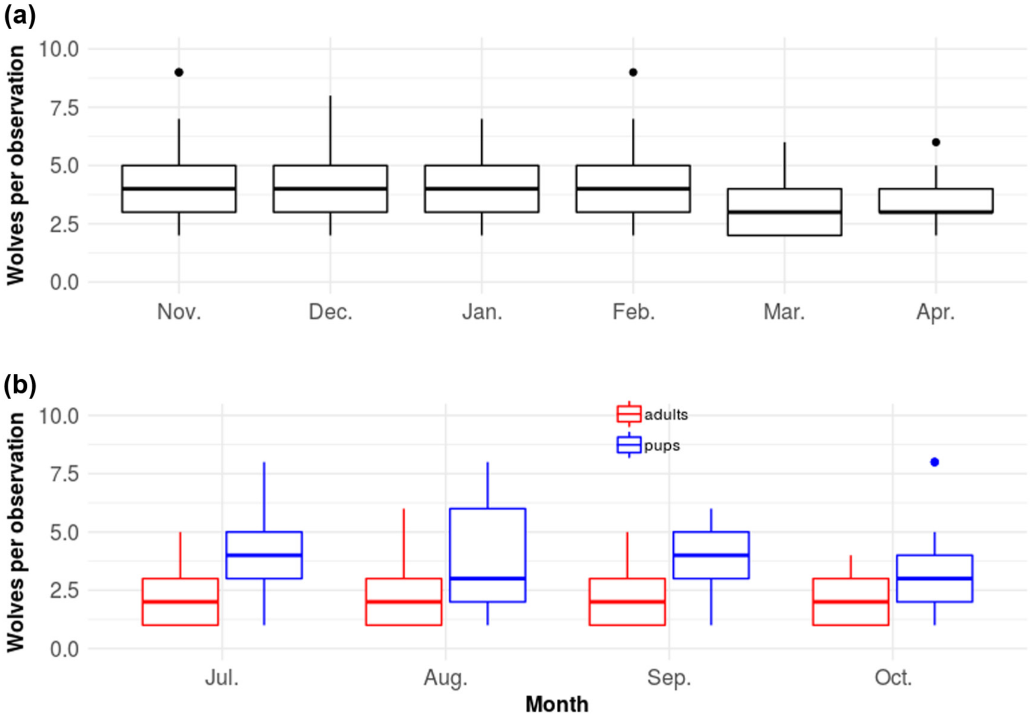

Figure 2. (A) Box plots of the number of wolves per observation in winter (n = 253 data), (B) box plot of number of adult/sub-adult wolves and pups per observation in summer at rendezvous sites (n = 186 and 150 for adults and pup, respectively).

(2019) with the data of the maximum number of wolves per pack in winter.

We considered pack-year as the unit to estimate average pack size: the social unit at a given locality and the year in which data were obtained (Apollonio et al. 2004, Jedrzejewski et al. 2007). In winter, data between November and the following April were assigned to a unique winter season. We estimated average pack size from the largest count in each pack during any given year, following Śmietana and Wajda (1997) and Jedrzejewski et al. (2000). The full data set is available in Supplementary material Appendix 1 Table A1.

Results

Winter

We obtained 253 winter records of travelling packs, at 42 localities, in 19 winters. Records per pack ranged 1–7 in any given winter, or pack-year (November 1999–April 2018, 160 pack-years). Individuals per pack ranged between 2 and 9 (Fig. 2A). Average number of wolves per pack was 4.2 ± 1.7 (± SD). The number of wolves per pack declined from 4.9 wolves (4.2–5.6, 95% CI) in November to 3.8 wolves (2.9–4.9, 95% CI) in April, based on the best model in Table 2. We found an effect of month on wolf counts per pack (Table 2), although the drop in average pack size was apparent in late winter (Fig. 2A). We found also a weak effect of 'method', and no effect of 'observer', 'year' or 'snow cover' on wolf counts (Table 2). Annual average pack size varied notably along the study period of 2000–2018 (Fig. 3), but we did not find a trend, or any significant autocorrelation in the maximum number of wolves per pack in winter (n = 160, Supplementary material Appendix 1 Fig. A1).

Summer

In summer, we obtained 237 observations of wolves at 22 localities, in 13 summers between 1990 and 2002 (43 pack-years). Observations per pack ranged 1–16 per year. We observed adults more frequently than pups (n = 186 and n = 150, respectively), and simultaneous observations of both adults and pups were rarer (n = 99). Adults and sub-adults ranged between 1 and 6 individuals per observation, whereas pups ranged between 1 and 8 (Fig. 2B). The largest pack observed in summer included 14 wolves: six adults and eight pups (full data set in Supplementary material Appendix 1 Table A1). The average number of adults/sub-adults per pack was 3.1 ± 1.3 (43 pack-years), while the average number of pups was 4.0 ± 1.9 (40 pack-years). The average total pack size in summer – estimated from simultaneous observations of both adults and pups – was 6.8 ± 2.5 (n = 99 observations; 31 pack-years). We did not find effects of 'month' or 'year' on the number of adults/sub-adults or of pups (Table 2). We did not find a trend in summer pack size along the study period.

Discussion

Our results of average pack size in winter (4.2 ± 1.7) were consistent with most European data, and even with reports along the south-eastern current range of the species in North America, e.g. Ontario and Wisconsin (Table 3). Summer estimates, on the other hand, showed much more variation, probably due at least partly to variability in methods. Winter methods seemed more consistent across studies and populations. Overall, we found wide variability in reporting certainty; several studies did not include the variance of

Table 2. Candidate models (GLMM, Poisson distribution, log link function, locality entered as random factor) fitted to number of wolves per pack in winter (n wolves n = 240), and n ads (n = 186) and n pups (n = 150) in summer. AIC indicates Akaike information criterion; ΔAIC is the difference between best model (lowest AIC) and candidate models; AICw are AIC weights. We included parameter estimates β and standard errors (SE) for the best winter model.

	AIC	ΔAIC	AICw
Winter			
month (cont.) + method	905.7	0	0.27
month (cont.)	906.1	0.4	0.22
month (factor)	906.9	1.2	0.15
method	907.8	2.1	0.09
null	907.9	2.2	0.09
year	908.2	2.5	0.08
snow cover	909.4	3.7	0.04
observer	909.6	3.9	0.04
	β ± SE	p	
intercept	1.64 ± 0.11		
month (cont.)	−0.05 ± 0.02	0.04	
method (snt)	−0.13 ± 0.08	0.11	
Summer			
n ads			
null	581.6	0	0.47
year	583.6	2	0.17
month (cont.)	583.6	2	0.17
month (factor)	583.6	2	0.17
n pups			
null	612.6	0	0.41
year	613.6	1	0.25
month (cont.)	614.3	1.7	0.17
month (factor)	614.5	1.9	0.15

their estimates (Table 3). Our dataset, based on a long series that used consistent methods, allowed reporting the variance of estimates, exploring changes in winter and summer wolf pack size, and evaluating some potential determinants of the counts. Note however that we obtained winter and summer data in relatively disjunct areas, where the staple diet of wolves is in principle different (Cuesta et al. 1991); therefore winter and summer estimates are not strictly comparable. North American data showed wider variation of winter pack size than European data (Table 3), probably reflecting wider variation in management of the studied populations (i.e. variation among years and zones in harvest and culling rates), and perhaps wider variation of prey base (Hayes and Gunson 1995, Fuller et al. 2003). Our winter estimates relied on so-called traveling packs, which have been implicitly regarded as roughly equivalent of actual pack size (Fuller et al. 2003). In winter, variation in pack cohesion may confound estimates of pack size based on traveling packs, especially in large ones (Peterson et al. 1984) that can split temporarily into foraging groups (Jedrzejewski et al. 2002). However, actual pack and traveling pack sizes do not differ significantly in winter, even in large packs (Dale et al. 1995). We expected high pack cohesion during winter in our study areas, as wolves must cope with unpredictable resources (mainly wild prey), both in space and time. Although it has been suggested that abiotic factors such as snow depth can affect cohesion (Fuller 1991), the most relevant factors affecting group cohesion are the same that drive group living in wolves, i.e. resource dispersion and competition with scavengers (Schmidt and Mech 1997, Vucetich et al. 2004, MacNulty et al. 2012, 2014). Usually high-ranking individuals do most kills, which means that few wolves commonly capitalize most predatory events (Sand et al. 2006), except when hunting very large prey

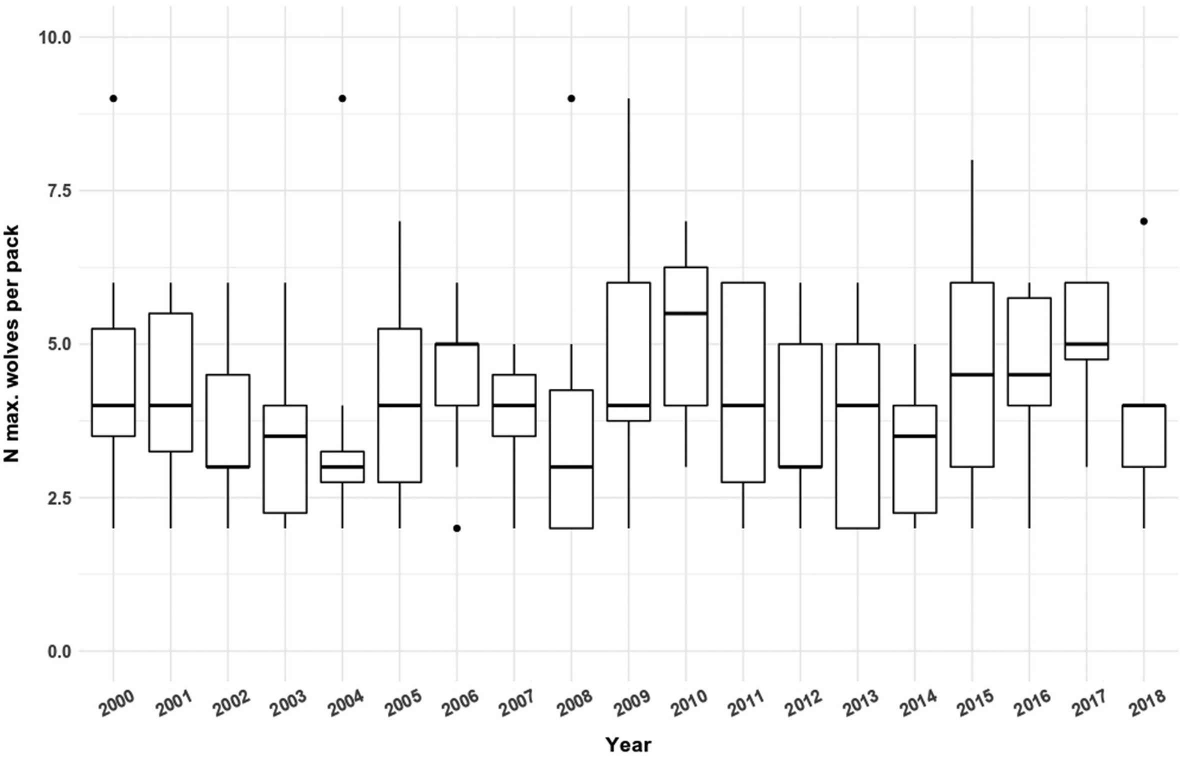

Figure 3. Box plot of winter pack size from 2000 to 2018. We used the highest count of each pack and year for the plot (n = 160 packs-year).

Table 3. Compilation of worldwide estimates of wolf pack size; mean ± SD (* indicates SE). We calculated averages where possible in those studies that did not provided them directly (see column Notes). DO = direct observation; EH = elicited howling; SNT = snow-tracking; Misc = miscellaneous; Q = questionnaires; RT = radio-tracking; TS = tracks; NIG = non-invasive genetic sampling. Column n indicates pack-years.

Eurasia	Method	Season	Pack size	n	Source	Notes
Apennines, IT	SNT	winter	3.7 ± 1.2	9	Ciucci and Boitani 1999	1 pack, 9 years: 3.8 (Oct.–Dec.) – 3.3. (Jan.–Apr.)
Apennines, IT	DO/EH/SNT	winter (Nov.–Apr.)	3.8 ± 1.1	19	Apollonio et al. 2004	
Bialowieza, PL-BY	DO/EH/RT/SNT	winter	3.8 (2.7–5.0)	29	Okarma et al. 1998; Table 1	3 winters
Białowieza, PL	DO/RT/SNT	winter	4.6 ± 1.8	31	Jedrzejewski et al. 2000	Largest pack size for a pack-winter; 4 packs, 11 years
Bialowieza, PL-BY	DO/EH/RT/SNT	winter	4.4 ± 1.0	16	Jedrzejewski et al. 2002	'Hunting group'; 4 packs, 4 winters
Bialowieza, PL-BY	RT/SNT	winter (Jan.–Mar.)	4.6 ± 1.0	11	Jedrzejewski et al. 2007; Table 2	4 packs, 4 years
Bialowieza, PL	DO/RT/SNT	winter (Nov.–Mar.)	3.8 ± 0.3 Nov. – 3.2 ± 0.2 Mar.	NA	Schmidt et al. 2008	4 packs, 5 years
Bieszczady, PL	SNT	winter (Nov.–Apr.)	5.6 (Nov.) – 3.9 (Apr.)	20	Smietana and Wajda 1997	Largest pack size for a pack; 5 packs, 4 winters
Bulgaria	Misc/Q	winter (Mar.)	2.7	159	Genov et al. 2010	≥ 1 wolf
Carpathian Mtns, PL	DO/SNT	winter	4.0 ± 1.5	25	Nowak et al. 2008	
Estonia	Q	winter (Nov.–Feb.)	4.6 (Nov.) – 2.1 (Feb.)	154	Valdmann et al. 2004	
Kazakhstan	DO/SNT	winter	4.2 (Oct.–Dec.) – 2.2 (Jan.–Feb.)	34	Heptner and Naumov 1998; Table 15	
Northern Spain	DO/SNT	winter (Nov.–Apr.)	4.2 ± 1.7; 4.9 (Nov.) – 3.8 (Apr.)	160	This study	Largest pack size for a pack-winter
Scandinavia, SE-NO	DO/SNT	winter	6.3 ± 1.6	21	Wabakken et al. 2001	Packs with confirmed reproduction
Scandinavia, SE-NO	DO/RT/SNT	winter (Nov.–Apr.)	4.1 ± 2.2	14	Sand et al. 2012	10 packs, 8 years
Apennines, IT	DO/EH	summer (May–Oct.)	4.4 ± 1.2	14	Apollonio et al. 2004	
Bialowieza, PL-BY	Misc/RT	summer (Sep.)	6.0 ± 1.3	11	Jedrzejewski et al. 2007; Table 2	4 packs, 4 years
Bulgaria	Misc/Q	summer–fall (Oct.)	4.7	159	Genov et al. 2010	≥1 wolf
Carpathian Mtns, PL	DO/EH/RT/TS	late summer	4.7 ± 1.8	21	Nowak et al. 2008	
Northern Spain	DO	summer (Jul.–Oct.)	3.1 ± 1.3 adults	43	This study	Largest pack size for a pack-summer
Northern Spain	DO	summer (Jul.–Oct.)	4.0 ± 1.9 pups	40	This study	Largest pack-size for a pack-summer
Apennines, IT	NIG	year round	5.6 ± 2.4	76	Caniglia et al. 2014	42 packs, 10 years
Israel	DO/RT	year round	3.2 ± 2.4	139	Hefner and Geffen 1999	'Foraging group'

North America	Method	season	Pack size	n	Source	Notes
North America	DO/RT/SNT	winter	5.9 ± 1.4	NA	Fuller et al. 2003; Table 6.3	Weighted mean of 33 studies
Alaska, US	DO/RT/SNT	winter	9.2 ± 3.2	12	Dale et al. 1995; Table 1	4 packs, 3 winters
Alberta, CA	DO/RT	winter (Feb.–Mar.)	8.6 ± 3.2	16	Kuzyk et al. 2006; Table 2	
Algonquin, ON, CA	DO/RT/SNT	winter (Feb.)	4.2 ± 1.5	14	Patterson et al. 2004; Table 1	
British Columbia, CA	SNT	late winter	6.4 ± 0.3	8	Bergerud and Elliot 1998	≥2 wolves, prior to culling
British Columbia, CA	SNT	late winter	4.4 ± 0.2	13	Bergerud and Elliot 1998	≥2 wolves, after culling

Table 3. Continued.

North America	Method	season	Pack size	n	Source	Notes
Brooks Range, AK, US	DO/RT/SNT	late winter (mid Apr.)	5.2 ± 3.0	72	Adams et al. 2008; Table 2	25 packs, 5 years
Idaho, US	Misc/RT	winter (year end)	8.0 ± 2.8	24	Ausband et al. 2014	≥2 wolves (2009)
Idaho, US	Misc/RT	winter (year end)	7.0 ± 3.4	20	Ausband et al. 2014	≥2 wolves (2010)
Ontario, CA	DO/RT/SNT	winter	4.3 ± 2.4	42	Kittle et al 2015; Supplementary material Appendix 1 Table A1	20 localities, 3 winters
Wisconsin, US	RT/SNT	winter	2.6 ± 0.9* – 5.2 ± 2.5*	1.092	Wydeven et al. 2009; Supplementary material Appendix 1 Table A2	28 years
Yukon, CA	DO/RT/SNT	winter (Jan.–Mar.)	2.7 ± 0.2* – 5.6 ± 0.6*	195	Hayes et al. 2003; Table 5	
Idaho, US	NIG	summer (Jun.–Aug.)	13.0 ± 6.0	5	Stenglein et al. 2011; Table 3	
Idaho, US	DO/RT	summer (Jul.–Sep.)	10.8 ± 2.7	5	Stenglein et al. 2011; Table 3	
Alberta, CA	DO/RT/SNT	fall	7.7 ± 2.8	NA	Webb et al. 2011	
Brooks Range, AK, US	DO/RT	fall	7.6 ± 4.0	63	Adams et al. 2008; Table 2	25 packs, 5 years

(MacNulty et al. 2014). A considerable proportion of individuals in packs are pups from the previous breeding season, which do not usually hunt but have to remain close to the others to access food. Indeed, most wolf populations subsist primarily on prey they hunt, and thus cohesion should be high when the group travels along the territory during the period not occupied in feeding the pups at rendezvous sites. It is conceivable that only where important resources are predictable, at least spatially (e.g. farm offal, which at the same time does not require refined hunting skills), wolf groups may show looser cohesion, even during winter (Boitani 1992).We found that average pack size declined 22% in winter, a decline that may be explained by mortality and dispersal (Fuller et al. 2003). Human-related mortality can cause marked population declines over the winter, yet our study is one of the few that followed intra-seasonal changes in wolf pack size (Mech 1977, Jedrzejewska et al. 1996, which showed lower and higher declines, respectively, compared with our study; see also Table 3). A decline in winter pack size may also be due to temporal separation of the breeding pair from the pack at the onset of the mating season, in late winter. We did find a slightly higher frequency of packs of two wolves in February–April compared to November–January (21%, n = 79 pack-years, and 15%, n = 81 pack-years, respectively; Supplementary material Appendix 1 Table A1), but we do not expect that temporal separation of breeding pairs fully explained the observed late winter decline in pack size. In addition, the overall frequency of winter packs composed by just two wolves in our study (18%, 160 pack-years) was somewhat lower than in other studies (e.g. 25% in Adams et al 2008; 31% in Kittle et al. 2015; metrics estimated from the data reported in both studies).

There were fewer estimates of summer wolf pack size in the literature (Table 3), despite that summer observations can provide estimates of reproductive success. Our summer estimates included only metrics from packs that bred successfully, i.e. those that raised pups to late summer. Thus they do not indicate average number of pups per pack because wolf populations include substantial though variable proportion of non-breeding and unsuccessful packs: 15% in protected areas without lethal management (e.g. Denali National Park, Alaska, Mech et al. 1998), and up to 20% in protected areas with some lethal management (Adams et al. 2008). Mitchell et al. (2008) found that smaller packs living in areas with high human-caused mortality rates in the Rocky Mountains of the U.S. had lower probability of raising pups, and there were between 16 and 28% of unsuccessful packs.

Monitoring wolf pack size while clearly reporting methods, sample sizes, season and determinants of seasonal and inter-annual changes, remains an important aspect of population dynamics of this highly social species (Liberg et al. 2012, Chapron et al. 2016). Non-invasive genetic sampling has been recently used to ease estimates of wolf abundance at moderate spatial scales (Marucco et al. 2009, Stransbury et al. 2014), and multiple methods of population monitoring had been recently proposed (Ausband et al. 2014, Jiménez et al. 2016). However, estimating and monitoring the number of wolves that cooperate in a given territory are elusive tasks (Stenglein et al. 2011), which would always benefit from the natural history insights of direct observations and counts of snow track sets in the diverse contexts of wolf populations (Table 3). Particularly so in those situations when more logistically complex or expensive procedures (genetic sampling, radio-telemetry) cannot be used to guide estimates. The importance of using robust estimates of wolf pack size is emphasized by the fact that wolf management in many populations worldwide relies on hunting and culling (Boitani 2003). Moreover, wolf culling programs were implemented in many areas with poor understanding of population dynamics and ecological effects (Gehring et al.

2003, Wallach et al. 2009, Rutledge et al. 2010, Creel et al. 2015), an scenario likewise suggested for the wolf population in Spain (Quevedo et al. 2019).

Acknowledgements – Funding – ER was supported by grant CGL 2017-83045-R AEI/FEDER UE.

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Supplementary material (available online as Appendix wlb-00594 at <www.wildlifebiology.org/appendix/wlb-00594>). Appendix 1.